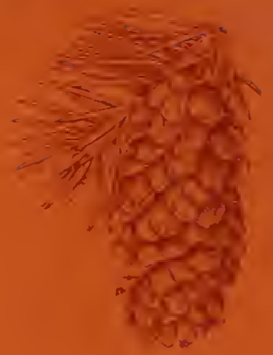
Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.

A99.9
F76Us
cy 3

GENETICS

# of SITKA SPRUCE



U.S. Department of Agriculture
Forest Service

Research Paper
WO-26

This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U. S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D. C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

Issued April 1975

CONTENTS

Page

RESEARCH SUMMARY iii
INTRODUCTION 1
NATURAL DISTRIBUTION AND HABITAT 2
PHYLOGENY AND TAXONOMY 3
    Intergeneric Crossability 4
    Interspecific Crossability 4
SEXUAL REPRODUCTION 6
    Controlled Pollination 6
    Seed Germination and Establishment 7
ASEXUAL REPRODUCTION 8
GENETICS 8
    Phenological Variation 8
    Morphological Variation 9
    Chemical and Cytological Variation 9
    Variation in Wood Characteristics 9
    European Provenance Studies 10
    Intra-Provenance Variation 10
BREEDING AND TREE IMPROVEMENT PROGRAMS 10
LITERATURE CITED 12

GENETICS OF SITKA SPRUCE [1]

Reference Abstract

Roche, L., and D. P. Fowler.
1975. Genetics of Sitka spruce. USDA For. Serv. Res. Pap. WO–26, 15 p.

Most tree-improvement work has been done in countries where Sitka spruce (*Picea sitchenis* (Bong.) Carr.) is a valuable exotic. Good information exists on provenance-level variation in early growth, dormancy, and frost susceptibility. Less is known about the details of inheritance of form, vigor, and wood quality attributes, although the available evidence indicates all can be genetically manipulated. B-chromosomes, and a clinal pattern of chromosome morphology, have been shown. Gene conservation within the native range and use of developing land races are important features of Sitka spruce breeding programs. A comprehensive research program is badly needed within the species' native range.

OXFORD: 174.7: *Picea sitchensis*: 165.3, 165.5, 165.7, 165.42
KEYWORDS: *Picea sitchensis*, Sitka spruce, genetics, tree improvement, adaptation

Research Summary
RP WO–26
April 1975

Review of about 100 references shows that most genetics research has been done in Britain and other countries where Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is planted as an important exotic. Very little information has been developed in the native range of coastal northwestern North America.

Reproduction is normally accomplished via seed, and techniques of controlled pollination, seed handling, and nursery culture are well established. Vegetative propagation occurs in nature via layering. Rooting of juvenile material may be a useful way to multiply genetically improved or inter-specific hybrid seedlings. Grafting has also proved feasible.

Provenance studies indicate well-defined patterns of heritable geographic variation in time of entering dormancy, height growth of young trees, frost susceptibility, total haploid chromosome length, nuclear volume, and, to a lesser degree, time of flushing.

Considerable variability has been reported in wood density, tracheid length, and spiral grain, as well as in various morphological features of cones (some of which are influenced by natural hybridization with white spruce). These findings suggest a basis for genetic interpretation and possible manipulation. B-chromosomes, unusual so far among gymnosperms, have been observed. Early studies on tree form and vigor indicate largely additive inheritance of form and more complicated inheritance of vigor, with inbreeding clearly resulting in growth depression.

Hybrids are possible with several other spruce species. They help elucidate evolutionary relationships, and at least two are commercially promising.

There is evidence that land races may already be developing among the exotic plantations, and breeding programs in these regions are taking advantage of selections from both the native range and adapted local plantations.

There is some urgency for gene conservation and ecological genetic studies of Sitka spruce within its native range, as some populations are being eliminated and others are being contaminated by both documented and undocumented non-local seedlings.

U.S. Department of Agriculture Forest Service

GENETICS OF SITKA SPRUCE[1]

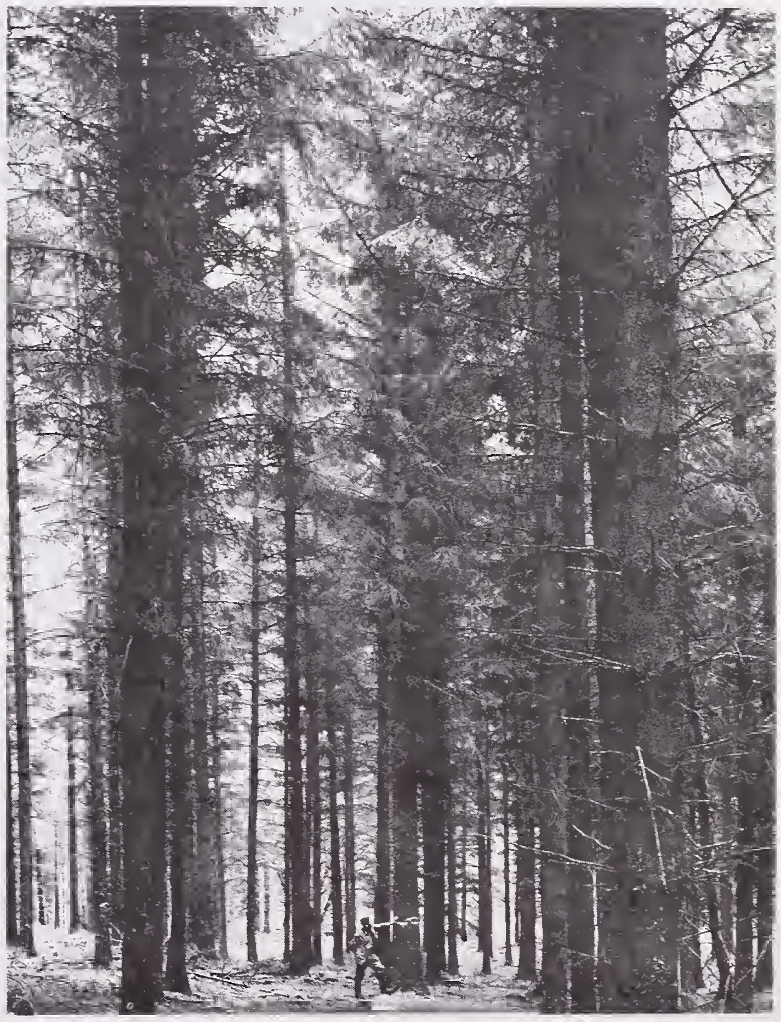
L. Roche[2] and D. P. Fowler[3]

INTRODUCTION

Sitka spruce, *Picea sitchensis* (Bong.) Carr., is a major timber and pulpwood species in the Pacific Northwest. While most *Picea* species occupy continental or montane habitats, Sitka spruce attains its maximum size in the fog belt of the coastal forests of Oregon, Washington, and British Columbia. Trees 250 ft. (76 m) in height and 10 ft. (3 m) in diameter are not uncommon (Garman 1953).

Although Sitka spruce is an important timber species in western North America, it is not an important reforestation species, and very little effort has been made to improve it genetically for use within its native range. On the other hand, it is the only North American spruce that has found wide acceptance as an exotic. It was introduced into Britain in 1831, and its performance from this and subsequent introductions led eventually to the establishment of plantations on a mass scale (fig. 1). Trees planted in 1846 have attained a height of 174 ft. (53 m), and an average annual height increment of 3 ft. (1 m) has been recorded in mature plantations on exceptional sites. On good sites in Britain, yields of up to 358 ft^3/ac/yr (25 m^3/ha/yr) can be attained, although average yield in stands less than 40 years of age is 167 ft^3/ac/yr (11.7 m^3/ha/yr) (Fletcher and Faulkner 1972). During the year 1969–1970, the national requirements for seed of Sitka spruce in Britain totalled 2,964 lb (1,334 kg). Seed procurement from local plantations during the same period was 1,011 lb. (459 kg) (Buszewicz 1970).

Sitka spruce is planted extensively in Ireland (Anonymous 1963), Norway (Borset 1967), and Denmark (Henricksen 1958) and is of considerable importance elsewhere in Europe (Schober 1962; LePont and Parde



F–522838

Figure 1.—Thriving, 40-year-old Sitka spruce plantation in Glenbrauter Forest, Argyll, Scotland. (Photograph supplied by L. W. Thomas, Forestry Commission, Great Britain.)

---

[1] The authors thank numerous correspondents in Europe and North America who forwarded information concerning the growth of Sitka spruce and programs of selection and breeding. Their contributions were most helpful.

[2] Head, Department of Forestry, University of Ibadan, Ibadan, Nigeria.

[3] Research Scientist, Canadian Forestry Service, Department of the Environment, Fredericton, N. B.

1962). It has also had some success in Iceland (Baxter 1956) and New Zealand (Thulin 1963).

It is in these countries, where Sitka spruce has proven to be a valuable exotic, that most of the tree improvement work has been carried out.

The objective of this paper is to review information on the genetics of the species and indicate approaches for further work.

For a detailed listing of all literature, the reader is referred to "Sitka spruce—a bibliography with abstracts," by A. S. Harris and R. H. Ruth (1970).

NATURAL DISTRIBUTION AND HABITAT

The native range extends as a narrow, 1,800 mile-long (2,880 km), coastal strip from the Kodiak Islands of Alaska into northern California (fig. 2). At maximum, this strip is 130 miles (210 km) wide (Ruth 1958).

In his "Silvical characteristics of Sitka spruce," Ruth (1958) describes the climatic, edaphic, physiographic, and biotic characteristics of the habitat. In summary, the species is restricted to the Pacific coastal fog belt. This habitat, while quite variable in some respects, is characterized by a long frost-free period, a superhumid climate of moderate temperature, and high precipitation. In general, the species does not occur in areas subject to extended periods of drought or subfreezing temperatures.

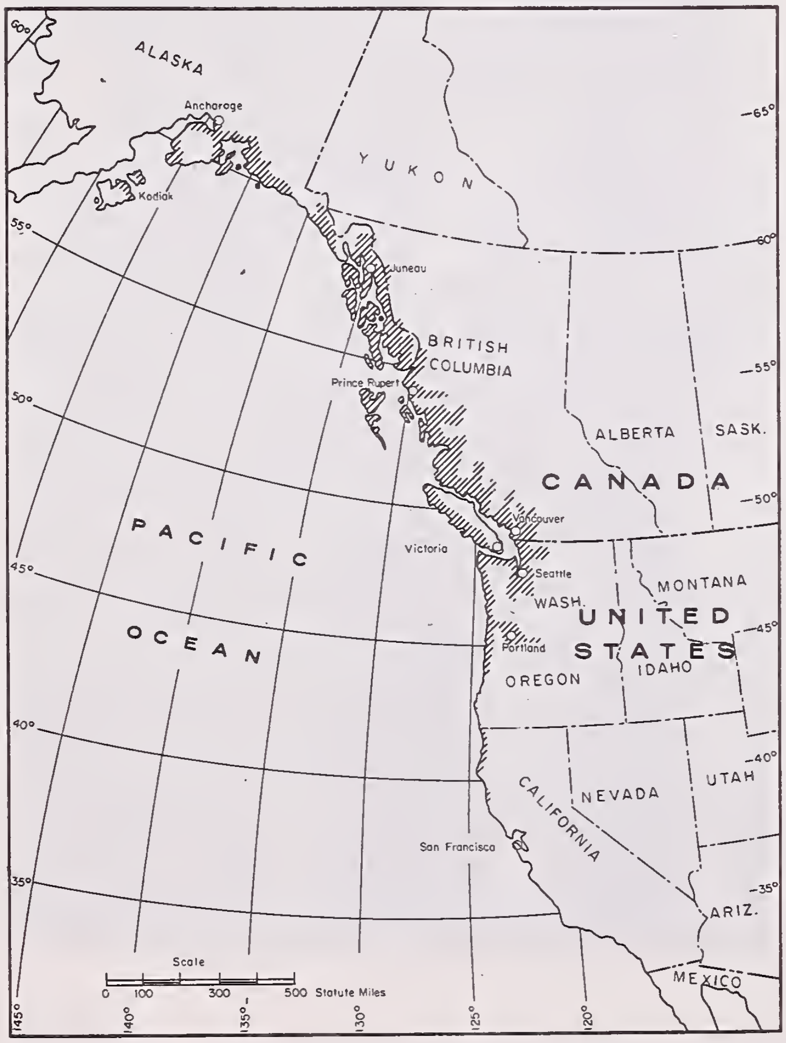


Figure 2.—Natural range of Sitka spruce (Ruth 1958; Daubenmire 1968).

Again in distinction from most other spruces, Sitka is a lowland tree. In the northern part of its range, it rarely grows above elevations of 1,000 ft. (300 m), and even there it is stunted. Further south in Alaska, it occasionally is found at 2,500 to 3,000 ft. (760 to 910 m). In its area of maximum growth in southern British Columbia and Washington, it is uncommon at elevations exceeding 1,000 ft. (300 m), while at the southern limit of the range merchantable trees are found only along coastal streams.

It is much less restricted by edaphic factors than by climate and physiography. It does well on soils derived from a wide range of parent materials. Though best development is on deep, medium-textured, mesic soils, it also grows on coarse soils or on those having a thick accumulation of organic material.

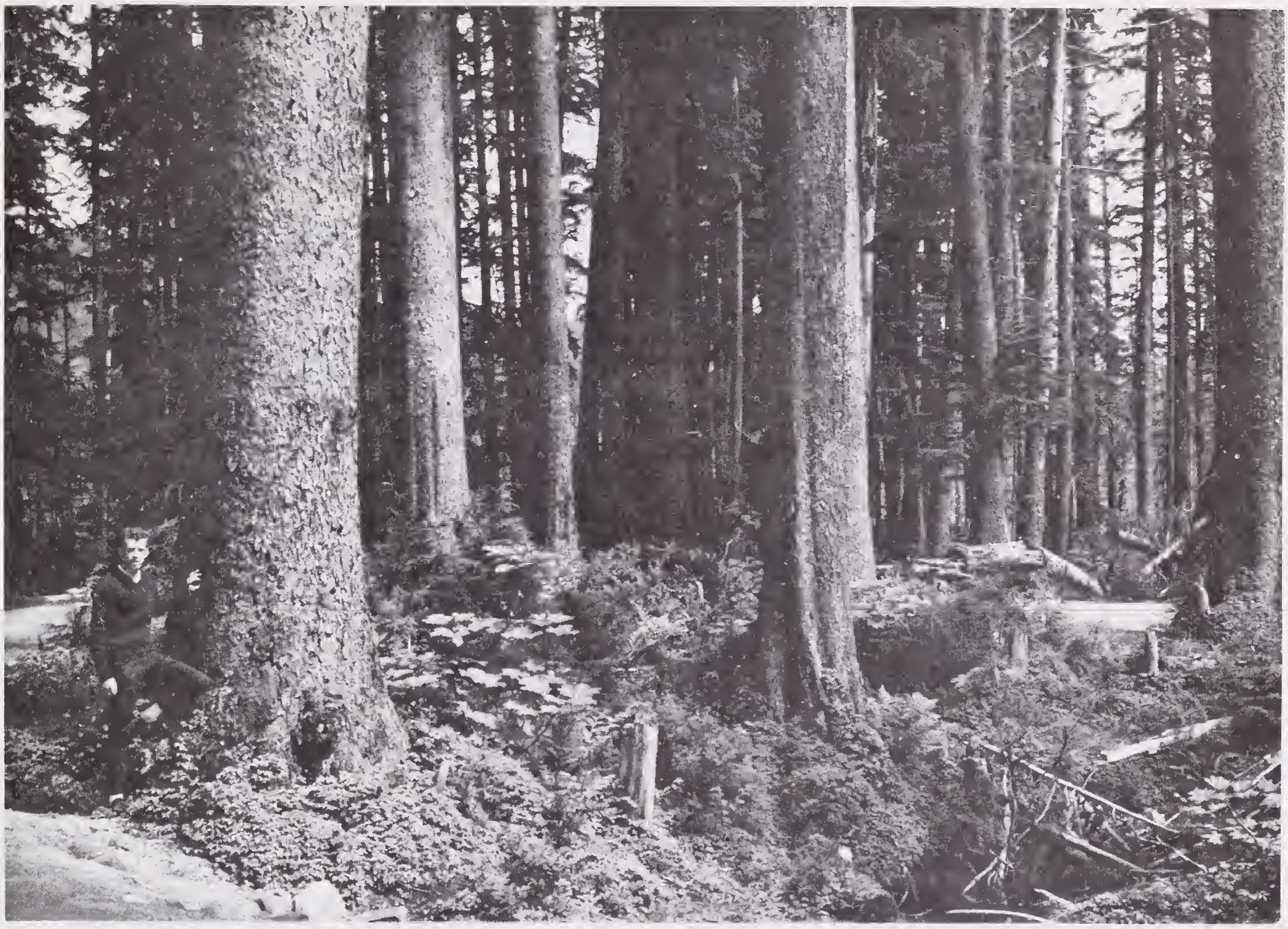
Along the Oregon and California coasts, it occupies dry sandy soils and dunes but does not attain merchantable dimensions (Harlow and Harrar 1950).

In Britain, it grows best in soil which is at least mildly acid, has a fairly high phosphorus content, and allows free rooting to a depth of at least 3 ft. (1 m). Moisture must be adequate throughout the year. Topographic effects, simply expressed as elevation, markedly affect growth, probably because of influences on water supply[4] and degree of exposure (Fourt 1968).

Pure stands are not uncommon. They are often found where recent land disturbance—e.g., by fire, landslide, or recent glacial recession—has created a pioneering habitat. Under more stable conditions, Sitka spruce is most commonly associated with western hem-

---

[4] Malcolm, D. C. 1971. Site factors and the growth of Sitka spruce. Rep. to Work. Group 6, IUFRO.



F-522839

Figure 3.—Virgin stand of Sitka spruce with some western hemlock and western redcedar. Fourteen miles (24 km) east of Prince Rupert, British Columbia, lat. 54° 15′, long. 130° 08′, elev. 500 ft. (150 m).

lock, *Tsuga heterophylla* (Raf.) Sarg. (fig. 3), but is also found in association with western redcedar, *Thuja plicata* Donn; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; red alder, *Alnus rubra* Bong.; and silver fir, *Abies amabilis* (Dougl.) Forbes. In the southern parts of its range, it is associated with Port-Orford-cedar, *Chamaecyparis lawsoniana* (A. Murr.) Parl., and redwood, *Sequoia sempervirens* (D. Don) Endl.

The only *Picea* associate is white spruce, *P. glauca* (Moench) Voss, which overlaps the eastern limit of Sitka distribution in Alaska and British Columbia. Natural hybridization occurs between these two species (Little 1953; Daubenmire 1968; Roche 1969).

PHYLOGENY AND TAXONOMY

Li (1953) suggested that the conifers originated around the periphery of the north Pacific basin. Wright (1955) supported this suggestion and proposed eastern Asia as the most probable site of origin of the spruces because of the large assortment of species found there—including *P. koyamai* Shiras., which is considered to be "primitive".

The genus *Picea* is of monophyletic origin (Wright 1955) in that even the most distantly related spruces are more similar to each other than to any species in any other genus. Many modern conifer families were differentiated 225 to 70 million years ago during the Mesozoic Era (Delevoryas 1962). The present-day spruces retain basic features that probably evolved toward the end of the Cretaceous Period (70 million years ago). Speciation would appear to have resulted from mutation at many loci, followed by recombination and drift or selection rather than by changes at a chromosomal level (Wright 1955). The haploid number of all species studied is 12, and the karyotypes are remarkably similar. The karyotype of Sitka differs from that of most other spruces in the occurrence of supernumerary (B) chromosomes (Moir and Fox 1972). The significance of these chromosomes is not well understood.

Intergeneric Crossability

In an attempt to elucidate the phylogeny of *Tsuga mertensiana* (Bong.) Carr., Van Campo-Duplan and Gaussen (1948) hypothesized that it is the intergeneric hybrid of *P. sitchensis* and *Tsuga heterophylla*. They proposed the name *Tsugo-Picea hookeriana* (Carr.) comb. nov. Other authors of the Toulouse school have reiterated the hypothesis and presented further evidence (Ferre 1952; Vabre-Durrieu 1954a, b; Chopinet 1962).

Duffield (1950) pointed out that hybrid swarms, the presence of which would support the hypothesis, have not been found in the sympatric portion of the ranges. He concluded that the crossability of *Tsuga* and *Picea* should be further tested, as had also been suggested by Van Campo-Duplan and Gaussen (1948). We are not aware of any comprehensive test of crossability between the two genera, and the nomenclature as proposed by the Toulouse school has not yet found general acceptance in the literature. Duffield's (1950) assessment of the hypothesis, therefore, continues to have force.

Interspecific Crossability

Natural hybridization between Sitka and white spruce in Alaska and British Columbia has been well documented (Little 1953; Garman 1957; Daubenmire 1968; Roche 1969). The interspecific hybrid has been described and named *Picea* x *lutzii* (Little 1953). In addition, hybridization occurs when white and Sitka spruce are planted in close proximity (Larsen 1934; Thaarup 1945; Bornebusch 1946). Hybrids are also found, although less frequently, when Serbian spruce (*Picea omorika* (Pancic) Purk.) and Sitka spruce are planted in the same location (Roulund 1971a). Natural hybrids between Sitka and Engelmann spruce, *P. engelmannii* Parry, have been reported (Garman 1957). Chemical studies by Hanover and Wilkinson (1970) verified the natural hybrids between Sitka and white spruce, but were inconclusive with respect to putative natural hybrids between Sitka and Engelmann.

Sitka has been crossed artifically with several other spruce species; the results are summarized in table 1. On the basis of crossability, Sitka appears closely related to *P. glauca, P. engelmannii,* and *P. jezoensis* (Sieb. and Zucc.), crossable with *P. omorika,* and only very distantly related to *P. abies* (L) Karst. and *P. asperata* Mast. Data on the other crosses are too limited to suggest relationships.

Wright (1955), in conjunction with his study of crossability, examined comparative morphology. Using 32 characters, he compiled a list of the number of characters (weighted) by which the spruces differ from one another. Numbers pertinent to Sitka are presented in table 1 and show only moderate agreement with the crossability data.

If the spruces originated in eastern Asia, then Sitka or an ancestor very probably reached North America via a land bridge between northeastern Asia and Alaska. The high crossability of white, Engelmann, and Sitka spruce suggests that speciation occurred after their establishment in North America. Because of its taxonomic similarity to Sitka, Wright (1955) considered *P. jezoensis* to be the most probable connecting link between Old World and western American spruces. Fowler (1966), however, suggested *P. glauca* as a more probable line because of the ease with which it crossed with the Asiatic *P. schrenkiana* Fisch. & Mey. and the poor success of *P. schrenkiana* x *P. jezoensis*. Subsequently, Hills and Ogilvie (1970) found fossil cones of a *P. glauca*-like spruce (*P. banksii*) in the Beaufort formation on northwestern Banks Island. They considered the formation to be of late Miocene or early Pleiocene origin (11 million years ago). They suggest *P. banksii* as an ancestor of all the North American spruces. While *P. banksii* could well be ancestral, the difficulty of crossing *P. mariana* (Mill.) B.S.P. and *P. rubens* Sarg. with *P. glauca* and the ease with which these species can be crossed with the European *P. omorika* oppose this hypothesis. *P. mariana* and *P. rubens* possibly reached North America in a separate migration from the west as suggested by Wright (1955), or may have arrived during the Tertiary Period (70 million years ago), before continent separation.

TABLE 1.—*Interspecific crosses of* Picea sitchensis *arranged in order of probable crossability*

× Other parent	Crossability	Authority [1]	Morphological [2] differences	Remarks
P. glauca	High	H–8,11,12,20,21:2,6,16 U–:5 F–:4	22	Closely related Natural hybrids Good seed yields
P. engelmannii	Probably high	H–6:1,7	14	Closely related Possibly natural hybrids No data on crossability
P. jezoensis	Moderately high	H–10,13,18:10,13,18 F–14	14	Closely related Moderate seed yield
P. omorika	Moderate	H–2,8,9,13,18,19 :7,10,15,18,22	24	Fairly closely related Seed yields moderate
P. breweriana	Moderate?	H–8,13:10	23	More crossing required to determine relationship
P. wilsonii	?	H–18	19	No data on putative hybrid
P. pungens	?	F–2	24	Possibly more closely related than indicated *pungens* crosses with *glauca*
P. likiangensis	?	U–3	22	No data on putative hybrids
P. abies	Low	H–8:17 F–3,14,18:18	24	Distantly related Seed yields very low
P. asperata	Low	F–3,18:2	20	Distantly related No successful crosses
P. maximowiczii	Low	F–3	19	No successful crosses
P. koyamai	Low	F–3	22	No successful crosses

H = Hybrid
U = Undetermined, putative hybrid
F = Failure

Authorities
1. Cheng 1939
2. Eklundh 1943
3. Faulkner et al. 1970
4. Heimburger 1954 (in Wright 1955)
5. Holst 1967 [3]
6. Jeffers 1971
7. Johnson 1939
8. Langner 1952
9. Langner 1959
10. Langner 1969
11. Larsen 1948
12. Little 1953
13. Maschning 1971 [4]
14. Mikkola 1969
15. Oksbjerg 1953
16. Rauter 1970
17. Rohmeder 1963, 1964
18. Roulund 1969
19. Roulund 1971
20. Schreiner 1937
21. Thaarup 1945
22. Vidakovic 1963

---

[1] Authorities listed after the colon (:) refer to reciprocal crosses or to crosses where direction is not known.
[2] From Wright (1955). Number of characters by which species differ from *P. sitchensis*; maximum possible difference is 53.
[3] Correspondence with M. J. Holst. Filed by Canadian Forestry Service, Fredericton, N.B.
[4] Correspondence with E. Maschning, Inst. Forstgenetik u. Forstpflanzenzüchtung. Filed by Canadian Forestry Service, Fredericton, N.B.

The fossil history of *Picea* in North America during the Pleistocene is incomplete. Daubenmire (1968) concluded that, before glaciation, Sitka spruce occupied roughly its present range. During glacial advances, its range was temporarily extended southward along the California coast beyond San Francisco Bay; the disjunct population now occurring in Mendocino County, California, is possibly a relict. Sitka spruce survived the last major glacial advance in coastal areas south of the glacier. Pre-Vashon pollen deposits on the Olympic Peninsula, close to the limit of pre-Wisconsin drift (>30,000 years ago) indicate that, during the middle and late Wisconsin glacial intervals, vegetation of the area resembled that found in coastal Alaska today (Heusser 1965). In addition, Daubenmire (1968) convincingly argues for the survival of this species on nunataks (hills or mountains surrounded by glaciers) well scattered along the coast from Puget Sound to Juneau. The most pertinent of the arguments for refuge occupation of nunataks relate to the rapid revegetation of the long coastal strip in British Columbia and Alaska after the near simultaneous deglaciation of the whole strip, and the interesting fact that Sitka spruce attains its biologically highest altitude (upper timberline) near its northerly limit.

SEXUAL REPRODUCTION

Sitka spruce is monoecious. Individual open-grown trees may reach sexual maturity in less than 20 years, but cone bearing in stands usually does not begin until age 20 to 40 (Ruth 1958). The number of cones increases with age and is greatest on dominant trees with well-developed crowns.

Except in the very northern portion of the range, good cone crops are produced at 3- to 4-year intervals with light crops intervening (USDA Forest Service 1948). Even where this species has been planted as an exotic, little difficulty in cone production has been encountered.

No information is available concerning the success of techniques to reduce age to flowering. The production of cones on sexually mature trees has been markedly increased by strangulating the bole with several wraps of thin iron wire (Linquist 1948). Applications of fertilizer have, to date, had inconclusive results (Faulkner et al. 1965).

The early stages of cone morphology have not been reported. Probably the pattern of initiation and development is similar to that of the closely related white spruce, with initiation occurring during the growing season preceding emergence of the reproductive structures. The suggestion of Faulkner et al. (1966), that early summer drought influences cone crops in the subsequent year, indicates that initiation takes place in early summer. In any event, ovulate and pollen strobili can be identified microscopically in the fall. In the next spring, the conspicuous, rose-red pollen strobili emerge and rapidly grow to 0.75 to 1 in. (1.9 to 2.5 cm) in length and 0.5 in. (1.3 cm) in diameter (Ruth 1958). As in the other spruces, the pollen strobili are in terminal positions on branchlets in the less vigorous portions of the crown. The ovulate strobili, which are erect, about 1 in. (2.5 cm) long and usually yellow-green tinged with red, develop on the previous year's internodes in the position of lateral buds. These strobili, although generally concentrated in the upper branches, may also occur throughout the crown.

In the central part of the species' range, pollen shed begins the last week in April and ends in the later part of May (Ruth 1958). No reliable information is available on the time of pollen shed and receptivity elsewhere, but probably the times are closely related to local climate. Phenology of bud flushing (and presumably of strobilus emergence) has been shown to differ by only 2 weeks in provenance trials including a wide diversity of population samples (Burley 1966a; Lines and Mitchell 1966).

After pollination, the ovulate strobili turn down and, during the next 4 months, mature into pale yellow-brown cones, 2.5 to 5 in. (6 to 13 cm) long. No published information is available on embryology, but probably it is similar to that of white spruce, which has been described by Mergen et al. (1965) and Rauter and Farrar (1969).

In the central part of the range, seed ripens about mid-September and cones begin to open in late September (Ruth 1958). Seedfall starts in middle to late October and is triggered by dry easterly winds. Usually, 90 percent of the seed has fallen by February of the next year (Ruth 1958).

Cones average 250 or more seeds apiece.[5] The seeds are small, ranging from 150 to 400 thousand/lb, (68 to 181 M/kg) and averaging 210 thousand/lb (95 M/kg) (USDA Forest Service 1948). Seed collected in Great Britain in 1956–1969 averaged 191,000/lb (87 M/kg), versus 174,000/lb (79 M/kg) for imported seeds.[5]

Controlled Pollination

Techniques for controlled pollination are basically the same as those reported by Wright (1962).

Although the ovulate buds can be distinguished microscopically in the fall or winter preceding emergence, such identification on a scale suitable for a controlled pollination program is not reliable. The ovulate buds can be identified with certainty only a few days or a week before the strobili push through the bud scales. Isolation bags are usually placed over branches bearing ovulate buds. In large-scale programs, it is sometimes necessary to bag branches that are in a position where ovulate buds are expected (Wright 1962).

Shaded and unshaded sausage casing, kraft paper, parchment paper, and terylene have been used for bags. We have tried several types, and those made of terylene—with or without windows—have proven to be most satisfactory on spruce. Terylene bags have also been successful in Great Britain (Faulkner et al. 1969; Samuel et al. 1972).

---

[5] Correspondence with A. G. Gordon, United Kingdom Forestry Commission, Alice Holt Forest Research Station, Farnham, Surrey, England, March 2, 1972, on file at Maritimes Forest Research Centre, Canadian Forestry Service, Fredericton, N.B.

Samuel et al. (1972) recognize five stages in the development of the ovulate strobili:

Stage 0. Resting, winter stage; strobili completely enclosed in bud scales.
Stage 1. Starting to elongate and becoming very pointed; no rupture of the bud scales (nonreceptive).
Stage 2. Elongating. Bud scales ruptured but possibly a cap of scales remaining(possibly receptive).
Stage 3. At intermediate elongated stage; scales fully open and almost horizontal (receptive).
Stage 4. Scales closing and strobili becoming slightly woody (nonreceptive).

Strobili should be pollinated when most are in Stage 3. As it is not unusual for strobili on the same branch to be in slightly different stages of development, and as all ovules of a strobilus do not reach maximum receptivity at the same time, seed set can be increased by pollinating once when most of the strobili are fully receptive and again 2 to 4 days later. In most spruce species, unpollinated strobili will remain receptive for several days.

The bags should be left in place for 10 to 20 days, or until all chance of contamination is over. We have found it desirable to leave bags (terylene) in place until the cones are harvested. This procedure saves time, simplifies relocation of the cones, and prevents loss from seedfall. If the bags are removed, it is usually desirable to rebag (perhaps with cloth or fiberglass screen) later (August) to prevent loss from rodents or by seed shedding.

Strobili can be collected a few days before pollen shed, when they are fully developed and beginning to dry. When squeezed between the thumb and forefinger the exudate should be granular in appearance and almost free of clear fluid. Pollen can be obtained somewhat earlier by "forcing." Almost any drying method that prevents contamination and avoids extremes of temperature is satisfactory. The dry pollen can be separated from the strobili by passing it through a 60 to 80 mesh/in (25 to 30 mesh/cm) screen. Fresh pollen is generally preferred, but pollen can be stored for at least 1 year at −18° C in a desiccator over silica gel.

Pollen will germinate in distilled water. Viability can be tested by agar or hanging-drop techniques (Wright 1962), or by germination on the surface of distilled water in sterile, cotton-stopped vials. Germination counts can be made after 48 to 72 hours at 24° C, but it does not necessarily follow that if pollen is viable *in vitro* it will also function *in vivo*.

Insects that attack strobili and cones may seriously interfere with any program of controlled pollination. Insecticide applications have generally been expensive and only partially satisfactory. We have found that a small piece (1 cm x 1 cm) of polyvinyl-chloride impregnated with Vapona[6] insecticide, placed in the isolation bag, is inexpensive and gives good control of several insect pests (Fowler 1971).

Seed Germination and Establishment

The USDA Forest Service, in its *Woody Plant Seed Manual* (1948), suggests that some lots of Sitka spruce require stratification for 60 to 90 days at −15 to −12° C in moist sand if they are to attain maximum germination. Heit (1961) recommended that seeds be germinated on a moist substratum subjected to alternating periods of 16 hours at 20° C in the dark and 8 hours at 30° C in low-intensity (at least 500 lux) light. Under these conditions, stratification is not required and germination is complete in 21 days. Germination is inhibited by temperatures below 20° C and by excessive moisture.

As optimum conditions for germination are seldom encountered in the nursery, it is advisable to sow beds in the fall or very early spring. If it is necessary to sow in late spring, the seeds should be stratified. Nursery practices suitable for other spruce species (USDA Forest Service 1948) are satisfactory for Sitka.

Under natural conditions, the seed will germinate on almost any bed that provides adequate moisture. Germination is best in mineral soil with side shade and overhead light, and it is generally unsatisfactory on deep moss or organic materials subject to severe moisture fluctuations (Ruth 1958). The major obstacle to seedling establishment is competing vegetation.

---

[6] Registered trademark: Shell Canada Ltd. 2, 2-dichlorovinyldimethylphosphate. This application is solely a research finding and not a registered use that has been approved by the U.S. Environmental Protection Agency. Mention of the trade name is for information only, and does not imply recommendation by the U.S. Department of Agriculture.

ASEXUAL REPRODUCTION

Layering occurs in Sitka spruce in natural stands (Cooper 1931). Faulkner et al. (1967a), noting that it also occurs in plantations on moist sites, assessed methods of propagating plus trees by this means. After 15 months, air-layers by the wedge-cut method were highly successful on two of three trees, while those made by a ring-wound technique were unsuccessful on the same three trees.

Stem cuttings can be rooted. Successes have ranged from a low value (Faulkner et al. 1967b) up to 100 percent (Griffith 1940; Larsen 1955). The difference probably reflects both the conditions under which the material was propagated and the genetic and nongenetic variability of the materials. Clones differ considerably in ability to root (Roulund 1971b) or graft. Furthermore, clones that graft with ease do not necessarily root with ease—and vice versa. Ease of propagation may be an important criterion for selecting plus trees (Faulkner et al. 1967b; Roulund 1971b).

The technique used by the United Kingdom Forestry Commission[7] is to collect current-year cuttings, two inches (5 cm) long, between late December and the end of February. The cuttings are cleanly cut at the base and soaked for several hours in an aqueous solution of 10 p/m IBA plus 10 p/m NAA in light. They are then set in coarse sand under intermittent mist, with the air temperature about 18°C, the bed temperature 24°C, and the day length about 20 hours. This technique is very successful with juvenile material. Older material is more difficult to root and may grow plagiotropically for a number of years.

The side-veneer method is the most common grafting technique for Sitka spruce in Britain (Faulkner et al. 1967b, 1969). The overall success is 45 percent, but it is thought that this percentage can be doubled if secondary scion material, collected from young grafts, is used instead of material from ortets.

GENETICS

Phenological Variation

Only in recent years has there been an attempt to make a major seed collection for genecological research throughout the range of Sitka spruce (Barner 1970; Falkenhagen 1971). Most of the information about genetic variation, therefore, is based on a few provenances. Taken together, however, these early investigations—the most comprehensive of which are by Burley (1964; 1965a, b; 1966a, b)—demonstrate a well-defined pattern of geographic variation.

A habitat-correlated, clinal pattern of variation associated with latitude has been clearly demonstrated for time of entering dormancy (Aldhous 1962; Burley 1966a; Lines and Mitchell 1966; Roche 1969; Lacaze 1970). Northern provenances are the first to enter dormancy, and the times to growth cessation and dormancy are positively correlated with total seasonal height growth (Lines and Aldhous 1957; Aldhous 1962; Thulin 1963; Burley 1966a; Roche 1969). In any given location, southern provenances enter dormancy later than northern. When moved north, southern provenances may continue growing long after frost injury becomes probable (Brandt 1970).

There is evidence that this pattern is photothermal (Robak 1957; Vaartaja 1959; Burley 1966a; Lines and Mitchell 1966; Roche 1969), and that the higher the latitude of the test site, the longer is the period of growth for given provenances (Lines and Mitchell 1966).

Genetic differences in time of flushing have not been so clearly demonstrated as those for time of growth cessation and dormancy. There is, nevertheless, some evidence that such differences may be important in determining the success of a given provenance in a particular region (Burley 1966a). Northern, high-elevation, and inland provenances are the first to flush and exhibit the most variation (Lines and Mitchell 1966). Thus, Burley (1966a) has shown that inland provenances from the Terrace, Kalum, and Nass Valleys in northwest British Columbia, together with inland sources from further north, flush earlier than coastal and southern provenances. It is likely that these early flushing inland provenances are from zones of hybridization between Sitka and white spruce (Garman 1957; Daubenmire 1968; Roche 1969).

---

[7] Correspondence with K. A. Longman, United Kingdom Forestry Commission, Edinburgh, Nov. 17, 1971, on file at Maritimes Forest Research Centre, Canadian Forestry Service, Fredericton, N.B.

Flushing in Sitka spruce appears to be predominantly a temperature rather than a photoperiod response (Aldhous 1962; Burley 1966a; Lines and Mitchell 1966; Roche 1969). Lines and Mitchell (1966) expressed the view that flushing differences between provenances are small, and that the irregular occurrence of spring frost makes them unimportant in Britain. Similar observations have been made by Brandt (1970) for Sitka provenances growing in Denmark. On the other hand, Lacaze (1970) suggested that selection for late flushing has occurred in Danish and French plantations and has resulted in the development of land races adapted to the local environment.

In practical silvicultural terms, the genetically based habitat-correlated, phenological variation indicates that (in the northern hemisphere and within the limits determined by chronic frost damage) it is preferable to transfer provenances north of their origin rather than south. To date, there are no published seed-transfer criteria for this species in its native range. In fact, seeding in California has typically been with provenances from the more northern stands in Oregon or even Washington.[8] When the species is to be grown outside its range, choice of provenances may determine success or failure. The international provenance trials established as a result of the seed collections made by the Danish Seed Center (Barner 1970) will in time provide detailed information about genetic variation within this species and its adaptability in diverse climatic regions outside the natural range.

Morphological Variation

Daubenmire (1968) found a north-south gradient in size of cone, length-width ratio of cone scale, sterigma (i.e., persistent needle base) angle, and phyllotaxy. He concluded that the morphologic gradient was probably clinal and correlated with a climatic gradient. Populations in the Skeena Valley of northwestern British Columbia exhibited morphological characteristics of both Sitka and white spruce, and were classified as hybrids. Toward the coast, the hybrid populations introgressed with Sitka spruce, and towards the interior with white spruce (Daubenmire 1968).

It seems clear that, in this region of white and Sitka spruce overlap, the variation in cone scale morphology is the result of hybridization (Garman 1957; Roche 1966, 1968, 1969; Daubenmire 1968). Subsequent selection and adaptation of the hybrid forms have produced a clinal pattern of variation that parallels the climatic changes from coastal to interior regions.

Chemical and Cytological Variation

Hanover and Wilkinson (1970), studying the chemical evidence for natural hybridization, concluded that Sitka spruce can be unequivocally distinguished from white and Engelmann spruce on the basis of three unidentified phenolic compounds that were absent from the foliage of Sitka spruce and consistently present in the other two species. Though the Sitka samples were diverse in origin, no chemical variation was observed. The authors concluded that two of the phenolic compounds provide a basis for determining the direction and possible degree of natural hybridization between Sitka and white spruce.

Burley (1965b) demonstrated a significant increase in haploid complement length and nuclear volume with increasing latitude of seed origin. His conclusions have been supported by Mergen and Thielges (1967), who showed that nuclear volume increases with latitude, and by Miksche (1971), who found that northern provenances have a higher DNA content. Moir and Fox (1972) discussed these findings in relation to their discovery of supernumerary (B) chromosomes in seed derived from eight provenances of Sitka spruce. They concluded that, until the effect of the B-chromosome is known, the exact significance of other variations in nuclear phenotype cannot be assessed. It is clear, nevertheless, that the pattern of variation revealed by chemical and cytological investigations parallels that determined by phenological and morphological studies.

Variation in Wood Characteristics

Attempts have been made to assess the variability of wood characteristics of provenances (Anonymous 1958; Jeffers 1959) and of single trees (MacGregor 1952; Stevens and Johnston 1961; Brazier 1967) grown in Britain on different sites (Stevens and Johnston 1961; Sunley and Lavers 1961) and in several regions (Bryan and Pearson 1955). Although no comprehensive heritability studies have been completed, it is evident that considerable variation in wood density, tracheid length, and spiral grain exists within provenances and that improvement in these characters is feasible.

---

[8] Correspondence with W. J. Libby, University of California, Berkeley, April 19, 1973, on file at Maritimes Forest Research Centre, Canadian Forestry Service, Fredericton, N.B.

Brazier (1967) reported that selection for vigor tends to favor trees of lower-than-average specific gravity but has no effect on tracheid length. He suggested that attention be directed to straight-grained trees having above-average wood density.

European Provenance Studies

Although Sitka spruce has been planted in western Europe for more than 100 years, detailed provenance studies in that region have only been undertaken during the last decade. Nevertheless, considerable information has accumulated, mostly from unreplicated planting trials or very young provenance tests.

Provenances from Queen Charlotte Island have generally proved the best on nearly all sites in Britain, though Alaskan provenances from south of latitude 59° 00′ are used on northern exposed sites and Washington provenances on favorable sites at low elevations. Provenances from southern Oregon and from California are susceptible to fall frosts, and Alaskan provenances generally grow very slowly, particularly those from north of latitude 59° 00′ (Faulkner et al. 1970; Lines 1970). O'Driscoll (1967) has recorded similar growth behavior for provenances growing in Ireland.

From observations of progenies in local plantations, it is suggested that plantations of Washington provenances be used as a short-term supply for Danish seed requirements. For special conditions, however,—for example, where Sitka spruce is to be used in shelterbelts or in recreation areas under very exposed conditions—Brandt (1970) suggests Alaskan provenances.

From a study (in a nursery near Nancy, France) of 24 provenances that included representatives from throughout the species' range as well as from Danish and French plantations, Lacaze (1970) tentatively recommended the northern Washington sources. Though exhibiting a long vegatative period, they were undamaged by early frost and showed considerable growth vigor. The two most southerly provenances, one from southern Oregon and the other from northern California, were severely damaged by fall frost.

The dearth of provenance information within the native range is most regretable, for Sitka spruce is potentially valuable for reforestation within the coastal fog belt.

Intra-provenance Variation

Very limited data are available on genetic variation of Sitka spruce at the individual-tree level. Faulkner et al. (1970) of the British Forestry Commission reported on a diallel crossing program carried out on seven 32-year-old trees selected for variability in form and growth habit. Early assessments (Samuel et al. 1972) indicated that characters chiefly affecting tree form are predominantly additive, while characters relating to vigor are under additive, dominance, and maternal control. In addition, progenies from self-pollination clearly exhibit a growth depression due to inbreeding.

BREEDING AND TREE IMPROVEMENT PROGRAMS

There are no published accounts of tree improvement programs with Sitka spruce in western North America, although industrial and other agencies have undertaken some work on a small scale. While Sitka spruce has been extensively logged, it has not been regenerated on a scale which would ensure perpetuation of the gene resource. Further, much of the seeding and planting has been with nonlocal seed, not documented as to origin (correspondence with Libby: see footnote 7). An improvement program is clearly needed, as is gene conservation *in situ* in parts of the range where continued exploitation is reducing the species to vestigial proportions (Roche 1971).

Sitka spruce is the most important commercial conifer in Britain and Ireland. Enough information has already been gained so that plantations established with improved seed of the correct provenance can be expected to outyield older plantings by 10 to 30 percent (Aldhous 1969). In the Forestry Commission's breeding program, up to 1,500 candidate plus trees are to be selected for growth rate, stem form, branching habit, freedom from disease and insect pests, and wood quality (Herbert 1971). Progeny tests are based on open pollinations or on artificial pollinations with a mixture from several selected trees (i.e. a polycross). Parents showing good general combining ability will subsequently be tested in specific combinations (Herbert 1971). A plan for the further improvement of Sitka spruce in Great Britain has recently been proposed by Fletcher and Faulkner (1972).

Techniques for early progeny-testing are being developed. Results to date suggest that tests in controlled environments are feasible and that the principal characters for wood production can be readily measured after one growing season. However, correlations between performance in controlled environments and in the field are yet to be determined (Herbert 1971). The possibility of using polyphenol analysis as a means of selecting vigorous individuals at an early age is also being investigated (Faulkner et al. 1972).

In Denmark, Sitka spruce exhibits a number of advantages over Norway spruce when the correct provenance is used. It is resistant to wind and salt spray, and grows well on poor soils—provided that moisture conditions are satisfactory. It develops well in many sand dune areas and on other sites where a topsoil of poor quality covers a more fertile subsoil (Brandt 1970).

Plantations have been established in Denmark over a period of 100 years, and progenies from them have frequently been superior in both growth and survival to progenies from imported seed of the same provenance. This evidence that land races have been developed is taken into consideration in the recent assessment (Brandt 1970) of the potential of the species for genetic improvement to meet Danish requirements and in a proposed improvement program based on this assessment. From good Danish stands of Washington origin, 200 plus trees will be selected for height growth, density of wood, stem form, branching habit, branch number, and resistance to drought, frost, wind, and insect damage.

Interspecific hybridization offers little promise where the pure species can be grown successfully. Its main value appears to be in increasing frost hardiness and possibly in extending the range of planting sites. At least two interspecific hybrids are promising enough to warrant further study. In Denmark, a program has been undertaken to produce hybrids between Sitka and Serbian spruce which will grow as well as or better than Sitka and will show improvement in characters such as frost hardiness, stem form, and branching (Roulund 1971a). The value of this hybrid, which is fairly expensive to mass-produce, would be greatly increased if methods of vegetative propagation could be developed (Brandt 1970).

The second interspecific hybrid is between white spruce and Sitka. To date there is no evidence that the hybrid is equal to Sitka in either form or growth rate. In Denmark, the hybrid is generally inferior to pure Sitka (Thaarup 1945), but Brandt (1970) suggests that if selected parents of correct provenance were used it should be possible to produce hybrids of value for specific sites. The silvicultural potential of this hybrid is presently being assessed under quite diverse conditions (Baxter 1956; MacGillivray 1962; Lines et al. 1966; Rauter 1970).

Sitka spruce is of some importance in the west of France (particularly in Brittany) and on the western slope of the Massif Central. From his studies of the progenies of trees in Danish and French plantations, Lacaze (1970) suggested that selection has occurred and that land races better adapted to the local environment than the original stock may have evolved.

In coastal regions of Norway, Alaskan provenances have generally proved to be the best adapted, and the highest quality stands are treated as seed-production areas. A selection program has been started, but no progeny tests have been made. The species has been propagated vegetatively in Norway by field-grafting on established rootstocks and, in good years, grafting success may reach 80 percent.

Although Sitka has been planted in other European countries, including Belgium, Holland, and Germany, no major tree improvement programs have been reported.

It may be concluded that genetic improvement is progressing well in those parts of the world where the species has found favor as an exotic. Aldhous (1969) may well be correct in his prediction of 10 to 30 percent increases in yield from plantations currently being established. Programs such as those presented by Brandt (1970) and Fletcher and Faulkner (1972) also appear to be sound. Each relies heavily on selection within provenances that have proven valuable in their new environments. The probable development of land races, as suggested by Brandt (1970) and Lacaze (1970), supports this approach. The infusion of new materials from as yet untested provenances is being considered and should facilitate the maintenance of a broad genetic base for the programs.

As has been indicated earlier, there is a paucity of work on genetics and breeding within the species' native range. Even the initial step of an improvement program, i.e., control of indiscriminate transfer of seeds and plant materials, has been neglected. A comprehensive program for Sitka spruce is badly needed in the northwestern United States and western Canada.

LITERATURE CITED

Anonymous.
1958. Report on the properties of four different provenance consignments of Sitka spruce. For. Prod. Res. Lab., Princes Risborough, England, 20 p.

Anonymous.
1963. Fo-roinn na foraoiseacta. [Minister for Lands, Report on Forestry.] Dublin 1962/63. 38 p.

Aldhous, J. R.
1962. Provenance of Sitka spruce; an account of the nursery stage of experiments sown in 1958. *In* Report on Forest Research for Year Ended March 1961, p. 147–154. G. B. For. Comm.

Aldhous, J. R.
1969. Looking forward: What timber should we grow and where. *In* Supplement to Forestry, p. 93–98.

Barner, H.
1970. *Picea sitchensis:* samples collected in 1968 and 1969. Circ. 6, Co-ordinating Centre of IUFRO Working Group on Procurement of Seed for Provenance Research. Humlebaek, Denmark.

Baxter, D. V.
1956. Skogar saga. Pac. Discovery 9: 9–14.

Bornebusch, C. H.
1946. Sitka-hvidgran-bastarden. [The Sitka × white spruce hybrid.] Dan. Skovforen. Tidsskr. 31: 42–46.

Borset, O.
1967. Om bruk av eksotiske treslag i Norge. [Use of exotic trees in Norway.] Skogbrukets Skogind. Forsk. (Oslo), 18 p.

Brandt, K.
1970. Statusopgorelse for Sitka spruce. [A status report for Sitka spruce.] Dan. Skovforen. Tidsskr. 55: 300–329. (*In* Danish. English transl. for British Forestry Commission, FCT 443, by L. Gombrich.)

Brazier, J. O.
1967. Timber improvement. I. A study of the variation in the wood characteristics in the young Sitka spruce. Forestry 40: 117–128.

Bryan, J., and F. G. O. Pearson.
1955. The quality of Sitka spruce grown in Great Britain. Empire For. Rev. 34: 144–153.

Burley, J.
1964. Variation in seed characteristics of Sitka spruce. Adv. Frontiers Plant. Sci. 10: 11–24.

Burley, J.
1965a. Genetic variation in *Picea sitchensis* (Bong.) Carr. A literature review. Commonw. For. Rev. 44: 47–58.

Burley, J.
1965b. Karyotype analysis of Sitka spruce, *Picea sitchensis* (Bong.) Carr. Silvae Genet. 14: 127–132.

Burley, J.
1966a. Genetic variation in seedling development of Sitka spruce *Picea sitchensis* (Bong.) Carr. Forestry 39: 68–94.

Burley, J.
1966b. Variation in colour of Sitka spruce seedlings. Q. J. For. 60: 51–54.

Buszewicz, G. M.
1970. Forest tree seed. *In* Report on Forest Research for Year Ended March 1970, p. 26–33, G. B. For. Comm.

Cheng, W. C.
1939. Les forets du Setchouan et du Si-kang oriental. [The forests of oriental Setchouen and Si-kang.] Trav. Lab. For. Univ. Toulouse 1: 1–233.

Chopinet, R.
1962. Les Tsuga et leurs hybrides. III. Especes d'origine hybride. [The hemlocks and their hybrids. III. Species of hybrid origin.] Rev. Hort. 134: 266–268.

Cooper, W. S.
1931. The layering habit in Sitka spruce and the two western hemlocks. Bot. Gaz. 91: 441–451.

Daubenmire, R.
1968. Some geographic variations in *Picea sitchensis* and their ecologic interpretation. Can. J. Bot. 46: 787–797.

Delevoryas, T.
1962. Morphology and evolution of fossil plants. Holt, Rinehart, and Winston, N. Y. 189 p.

Duffield, J.
1950. Review of "Sur quatre hybrides de genres chez les Abietinees", by M. Van Campo-Duplan and H. Gaussen. J. For. 48: 440.

Eklundh, C.
1943. Artkorsninger inon sl. *Abies*, *Pseudotsuga*, *Picea*, *Larix*, *Pinus* och *Chamaecyparis*, tillhorande fam. Pinaceae. [Hybrids within the genera *Abies*, *Pseudotsuga*, *Picea*, *Larix*, *Pinus* and *Chamaecyparis* belonging to the family Pinaceae.] Sven. Rapp. Tidn. 46: 55–61, 101–105, 130–133.

Falkenhagen, E. R.
1971. A study of the IUFRO Sitka spruce provenances and single tree progenies. Proc. 13th Meet. Comm. For. Tree Breed. Can., p. 131–132.

Faulkner, R., R. B. Herbert, and A. M. Fletcher.
1965. Forest genetics. *In* Report on Forest Research for the Year Ended March 1964, p. 53–56. G. B. For. Comm.

Faulkner, R., R. B. Herbert, and A. M. Fletcher.
1966. Forest genetics. *In* Report on Forest Research for the Year Ended March 1965, p. 59–60. G. B. For. Comm.

Faulkner, R., R. B. Herbert, A. M. Fletcher.
1967a. Forest genetics. *In* Report on Forest Research for the Year Ended March 1966, p. 67–68. G. B. For. Comm.

Faulkner, R., R. B. Herbert, and A. M. Fletcher.
1967b. Forest genetics. *In* Report on Forest Research for the Year Ended March 1967, p. 92–93. G. B. For. Comm.

Faulkner, R., R. B. Herbert, and A. M. Fletcher.
1969. Forest genetics. *In* Report on Forest Research for the Year Ended March 1969, p. 101–105. G. B. For. Comm.

Faulkner, R., A. M. Fletcher, K. A. Longman, and R. C. B. Johnstone.
1970. Forest genetics. *In* Report on Forest Research for the Year Ended March 1970, p. 106–113. G. B. For. Comm.

Faulkner, R., A. M. Fletcher, R. C. B. Johnstone, and G. I. Forrest.
1972. Biochemical variation. *In* Report on Forest Research for the Year Ended March 1972, p. 76–82. G. B. For. Comm.

Ferré, Y. de.
1952. Les formes de jeunesse des Abietacees: ontogenie-phylogenie. [The juvenile forms of the Abietaceae: ontogeny-phylogeny.] Fac. Sci. Toulouse, vol. 1, et Trav. Lab. For. Univ. Toulouse, vol. (2) : art. 1, 282 p.

Fletcher, A. M., and R. Faulkner.
1972. A plan for the improvement of Sitka spruce by selection and breeding. G. B. For. Comm., Res. Dev. Pap. 85, 31 p.

Fourt, D. F.
1968. Sitka spruce, shelter and moisture. G. B. For. Comm., Res. Dev. Pap. 72, 8 p.

Fowler, D. P.
1966. A new spruce hybrid—*Picea schrenkiana* x *P. glauca*. Proc. 2nd Genet. Workshop Soc. Amer. For. and 7th Lake States For. Tree Improve. Conf. 1965, p. 44–47. USDA For. Serv. Res. Pap. NC–6. North Central Forest Experiment Station, St. Paul, Minn.

Fowler, D. P.
1971. A technique for controlling insect damage in pollination bags. Can. J. For. Res. 1: 66–67.

Garman, E. H.
1953. Pocket guide to the trees and shrubs of British Columbia. Ed. 2. B.C. For. Serv. Publ. B. 28, 102 p.

Garman, E. H.
1957. The occurrence of spruce in the interior of British Columbia. B.C. For. Serv., Tech. Publ. T49, 31 p.

Griffith, B. G.
1940. Effect of indolebutyric acid, indoleacetic, and alpha naphthaleneacetic acid on rooting of cuttings of Douglas-fir and Sitka spruce. J. For. 38: 496–501.

Hanover, J. W., and R. C. Wilkinson.
1970. Chemical evidence for introgressive hybridization in *Picea*. Silvae Genet. 19: 17–22.

Harlow, W. M., and E. S. Harrar.
1950. Textbook of dendrology, covering the important forest trees of the U.S.A. and Canada. Ed. 3. McGraw-Hill, N.Y. 555 p.

Harris, A. S., and R. H. Ruth.
1970. Sitka spruce—a bibliography with abstracts. USDA For. Serv. Res. Pap. PNW–105, 251 p. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Heit, C. E.
1961. Laboratory germination and recommended testing methods for 16 spruce *Picea* species. Proc. Assoc. Off. Seed Anal. N. Am. 51: 165–171.

Henriksen, H. A.
1958. Sitkagranens vaest og sundhedstilstend i Danmark. [Increment and health of Sitka spruce in Denmark.] Forstl. Forsogsvaes. 24: 1–372. [English summary.]

Herbert, R. B.
1971. Development of glasshouse techniques for early progeny test procedures in forest tree breeding. G. B. For. Comm., For. Rec. 74, 34 p.

Heusser, C. J.
1965. A Pleistocene physiographical sketch of the Pacific Northwest and Alaska. *In* The Quarternary of the United States, p. 469–483. Ed. H. E. Wright, Jr., and D. G. Frey. Univ. Press, Princeton, N.J.

Hills, L. V., and R. T. Ogilvie.
1970. *Picea banksii* n. sp. Beaufort Formation (Tertiary), Northwestern Banks Island, Arctic Canada. Can. J. Bot. 48: 457–464.

Jeffers, J. N. R.
1959. Regression models of variation in specific gravity in four provenances of Sitka spruce. J. Inst. Wood. Sci. 4: 44–59.

Jeffers, R. M.
1971. Research at the Institute of Forest Genetics, Rhinelander, Wisconsin. USDA For. Serv., Res. Pap. NC–67, 31 p. North Central Forest Experiment Station, St. Paul, Minn.

Johnson, L. P. V.
1939. A descriptive list of natural and artificial interspecific hybrids in North American forest tree genera. Can. J. Res. (C) 17: 411–444.

Lacaze, J. F.
1970. Comportement de diverses provenances d'epicea de Sitka en France. [Behavior of different provenances of Sitka spruce in France.] Rev. For. Fr. 22: 45–54.

Langner, W.
1952. Die Forschungsstatte fur Forstgenetik und Forstpflanzenzuchtung in Schmalenbeck. [Forest genetic and tree breeding research at Schmalenbeck.] Z. Weltforstwirtsch. 15: 15–18.

Langner, W.
1959. Ergebnisse Einiger Hybridisierrungsversuche Zwischen *Picea sitchensis* (Bong.) Carr. und *Picea omorika* (Pancic) Purkyne. [Results of some trials of hybridization between *Picea sitchensis* (Bong.) Carr. and *Picea omorika* (Pancic) Purkyne.] Silvae Genet. 8: 138–143. [English summary].

Langner, W.
1969. Some cases of inbreeding and hybrid weakness. 2nd World Consult. For. Tree Breeding, FAO, p. 903–912.

Larsen, C. M.
1955. The seasonal variation in the natural rooting capacity of cuttings of Norway spruce and Sitka spruce. Z. Forstgenet. 4: 69–80.

Larsen, C. S.
1934. Forest tree breeding. R. Vet. and Agric. Coll. Yearb., p. 93–113. Copenhagen, Denmark.

Larsen, C. S.
1948. Arboretet i Horsholm og Forstbotanisk have i Charlottenlund 1948. [Horsholm Arboretum and Forest Botanical Garden 1948.] Foren. Dendrol. Parkvard Arsb. Lunstgarden 1947–48: 1–76.

LePont, P., and J. Parde.
1962. Les resineux dans le nord de la Seine-Maritime. [Conifers in the north of Seine-Maritime.] Rev. For. Fr. 14: 979–993.

Li, H. L.
1953. Present distribution and habitats of the conifers and taxads. Evolution 7: 245–261.

Lindquist, B.
1948. Genetics in Swedish forestry practice. Chronica Botanica Co., Waltham, Mass. 173 p.

Lines, R.
1970. Notes on provenance of coniferous forest tree seed for use in Scotland. Scot. For. 24: 10–12.

Lines, R., and J. R. Aldhous.
1957. Provenance studies. *In* Report on Forest Research for the Year Ended March 1957, p. 51–58. G. B. For. Comm.

Lines, R., and A. F. Mitchell.
1966. Differences in phenology of Sitka spruce provenances. *In* Report on Forest Research for the Year Ended March 1965, p. 173–184. G. B. For. Comm.

Lines, R., S. A. Newstein, O. W. Henman, and J. A. Herson.
1966. Species trials. *In* Report on Forest Research for the Year Ended March 1965, p. 33–34. G. B. For. Comm.

Little, E. L., Jr.
1953. A natural hybrid in Alaska. J. For. 51: 745–747.

MacGillivray, H. G.
1962. Report on tree improvement at Acadia Forest Experiment Station. Proc. 8th Meet. Comm. For. Tree Breed. Can., p. 1–14.

MacGregor, W. D.
1952. Sitka spruce-density survey project. G. B. For. Prod. Res. Lab., Prog. Rep. 1, 6 p.

Mergen, F., J. Burley, and G. M. Furnival.
1965. Embryo and seed development in *Picea glauca* (Moench) Voss after self-, cross-, and wind-pollination. Silvae Genet. 14: 188–194.

Mergen, F., and B. A. Thielges.
1967. Intraspecific-variation in nuclear volume in four conifers. Evolution 21: 720–724.

Mikkola, L.
1969. Observations on interspecific sterility in *Picea*. Ann. Bot. Fenn. 6: 285–339.

Miksche, J. P.
1971. Intraspecific variation of DNA per cell between *Picea sitchensis* (Bong.) Carr. provenances. Chromosoma 32: 343–352.

Moir, R. B., and D. F. Fox.
1972. Supernumerary chromosomes in *Picea sitchensis* (Bong.) Carr. Silvae Genet. 21: 182–186.

O'Driscoll, J.
1967. Tree improvement. For. Res. Rev., p. 12–21. For. Div., Dep. Lands, Ireland.

Oksbjerg, E.
1953. Om *Picea omorika*. [Notes on *Picea omorika*.] Dan. Skovforen. Tidsskr. 38: 179–192.

Rauter, R. M.
1970. Spruce breeding program at the Southern Research Station, Maple, Ontario. Proc. 12th Meet. Comm. For. Tree Breed. Can., p. 47–51.

Rauter, R. M. and J. L. Farrar.
1969. Embryology of *Picea glauca* (Moench) Voss. Proc. 16th Northeast. For. Tree Improve. Comm., p. 13–24.

Robak, H.
1957. Sambandet mellom daglengden og avslutningen av den arlige vekstperioden hos en del naletreslag av interesse for vart skogbruk. [Relation between day length and the end of the annual growth period in some conifers of interest to Norwegian Forestry.] Medd. Vestl. Forstl. Fors kssia. 31: 62. [English summary.]

Roche, L.
1966. Spruce provenance research in British Columbia. Proc. 10th Meet. Comm. For. Tree Breed. Can., p. 107–121.

Roche, L.
1968. Introgressive hybridization in the spruce species of British Columbia. Proc. 11th Meet. Comm. For. Tree Breed. Can., p. 249–269.

Roche, L.
1969. A genecological study of the genus *Picea* in British Columbia. New Phytol. 68: 504–554.

Roche, L.
1971. The conservation of forest gene resources in Canada. For. Chron. 47: 215–217.

Rohmeder, E.
1963. Experiments on forest tree hybrids in Bavaria from 1936 to 1962. World Consult. For. Genet. Tree Improve., Stockholm. 26/1.

Rohmeder, E.
1964. [Breeding research on Norway spruce in Bavaria.] Mitt. Staatsforstverwalt. Bayerns, No. 34, p. 7–27. (For. Abstr. 25(4): 4671. 1969.)

Roulund, H.
1969. Artskrydsningsforsog i slaegten Picea. [Species crossing experiment in the genus *Picea*.] Dan. Skovfor. Tidsskr. 54: 222–233. [English summary.]

Roulund, H.
1971a. Observations on spontaneous hybridization in *Picea omorika* (Pancic) Purkyne. Forest Tree Improvement No. 2. Arboretet, Horsholm, p. 2–17.

Roulund, H.
1971b. Experiments with cuttings of *Picea abies*, *Picea sitchensis* and the hybrid *Picea omorika* x *Picea sitchensis*. Forest Tree Improvement No. 3. Arboretet, Horsholm, p. 25–57.

Ruth, R. H.
1958. Silvical characteristics of Sitka spruce. USDA For. Serv., Pac. Northwest For. and Range Exp. Stn., Silvical ser. 8, 19 p. Portland, Oreg.

Samuel, C. J. A., R. C. B. Johnstone, and A. M. Fletcher.
1972. A diallel cross in Sitka spruce with assessment of first-year characters in an early greenhouse test. Theoret. Appl. Genet. 42: 53–61.

Schober, R.
1962. Die Sitka-Fichte. Eine biologisch-ertragskundliche Untersuchung. [Sitka spruce. A study of its biology and yield.] Schr. Reihe Forstl. Fak. Univ. Gottingen 24/25. 230 p. [English summary.]

Schreiner, E. J.
1937. Improvement of forest trees. USDA Yearb. 1937, p. 1242–1279 (+16 p. bibliography).

Stevens, W. C., and D. D. Johnston.
1961. The seasoning properties of home-grown Sitka spruce. J. Inst. Wood Sci. (London) 7: 28–33.

Sunley, J. P., and G. M. Lavers.
1961. Variation in the strength and specific gravity of Sitka spruce grown in Great Britain. J. Inst. Wood Sci., London 7: 15–27.

Thaarup, P.
1945. Bastarden sitkagran × hvidgran. [The hybrid Sitka spruce × white spruce.] Dan. Skovfor. Tidsskr. 30: 381–384.

Thulin, I. J.
1963. Forest tree improvement. N. Z. For. Serv. Rep. For. Res. Inst. 1962, p. 36–39.

USDA Forest Service
1948. Woody-plant seed manual. USDA For. Serv. Misc. Publ. 654, 416 p.

Vaartaja, O.
1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monogr. 29: 91–111.

Vabre-Durrieu, A.
1954a. L'hybride *Tsugo-Picea hookeriana* et ses parents: etude des plantules. [The hybrid *Tsugo-Picea hookeriana* and its parents: study of the seedlings.] Trav. Lab. For. Univ. Toulouse 1, Vol. 5, art. 15. 8 p.

Vabre-Durrieu, A.
1954b. L'hybride *Tsugo-Picea hookeriana* et ses parents: etude chromosomique et caryologique. [The hybrid *Tsugo-Picea hookeriana* and its parents: a chromosomal and karyological study.] Trav. Lab. Forest. Univ. Toulouse 1, vol. 5, art. 17, 4 p.

Van Campo-Duplan, M., and H. Gaussen.
1948. Sur quatre hybrides de genres chez les Abietinees. [Four intergeneric hybrids among the Abietineae.] Trav. Lab. For. Univ. Toulouse 1, vol. 4: art. 24, 14 p.

Vidakovic, M.
1963. Meduvrsno krizanje Panciceve omorike (*Picea omorica* (Pancic) Purkyne) sa Sitkanskom smrcom (*Piceae sitchensis* (Bong.) Carr.). [Interspecific crossing between Serbian spruce (*Picea omorica* (Pancic) Purkyne) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.).] Sumarstvo 10–12: 337–342. [English summary].

Wright, J. W.
1955. Species crossability in spruce in relation to distribution and taxonomy. For. Sci. 1: 319–349.

Wright, J. W.
1962. Genetics of forest tree improvement. FAO For. and For. Prod. Stud. 16. 399 p.

☆ U.S. GOVERNMENT PRINTING OFFICE: 1975 O—552-699

Roche, L., and D. P. Fowler.
1975. Genetics of Sitka spruce. USDA For. Serv. Res. Pap. WO–26, 15 p.

Most tree-improvement work has been done in countries where Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is a valuable exotic. Good information exists on provenance-level variation in early growth, dormancy, and frost susceptibility. Less is known about the details of inheritance of form, vigor, and wood quality attributes, although the available evidence indicates all can be genetically manipulated. B-chromosomes, and a clinal pattern of chromosome morphology, have been shown. Gene conservation within the native range and use of developing land races are important features of Sitka spruce breeding programs. A comprehensive research program is badly needed within the species' native range.

OXFORD: 174.7: *Picea sitchensis:* 165.3, 165.5, 165.7, 165.42
KEYWORDS: *Picea sitchensis*, Sitka spruce, genetics tree improvement, adaptation

---

Roche, L., and D. P. Fowler.
1975. Genetics of Sitka spruce. USDA For. Serv. Res. Pap. WO–26, 15 p.

Most tree-improvement work has been done in countries where Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is a valuable exotic. Good information exists on provenance-level variation in early growth, dormancy, and frost susceptibility. Less is known about the details of inheritance of form, vigor, and wood quality attributes, although the available evidence indicates all can be genetically manipulated. B-chromosomes, and a clinal pattern of chromosome morphology, have been shown. Gene conservation within the native range and use of developing land races are important features of Sitka spruce breeding programs. A comprehensive research program is badly needed within the species' native range.

OXFORD: 174.7: *Picea sitchensis:* 165.3, 165.5, 165.7, 165.42
KEYWORDS: *Picea sitchensis*, Sitka spruce, genetics, tree improvement, adaptation

---

Roche, L., and D. P. Fowler
1975. Genetics of Sitka spruce. USDA For. Serv. Res. Pap. WO–26, 15 p.

Most tree-improvement work has been done in countries where Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is a valuable exotic. Good information exists on provenance-level variation in early growth, dormancy, and frost susceptibility. Less is known about the details of inheritance, although the available evidence indicates all can be genetically manipulated. B-chromosomes, and a clinal pattern of chromosome morphology, have been shown. Gene conservation within the native range and use of developing land races are important features of Sitka spruce breeding programs. A comprehensive research program is badly needed within the species' native range.

OXFORD: 174.7: *Picea sitchensis:* 165.3, 165.5, 165.7, 165.42
KEYWORDS: *Picea sitchensis*, Sitka spruce, genetics, tree improvement, adaptation

---

Roche, L., and D. P. Fowler.
1975. Genetics of Sitka spruce. USDA For. Serv. Res. Pap. WO–26, 15 p.

Most tree-improvement work has been done in countries where Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is a valuable exotic. Good information exists on provenance-level variation in early growth, dormancy, and frost susceptibility. Less is known about the details of inheritance of form, vigor, and wood quality attributes, although the available evidence indicates all can be genetically manipulated. B-chromosomes, and a clinal pattern of chromosome morphology, have been shown. Gene conservation within the native range and use of developing land races are important features of Sitka spruce breeding programs. A comprehensive research program is badly needed within the species' native range.

OXFORD: 174.7: *Picea sitchensis:* 165.3, 165.5, 165.7, 165.42
KEYWORDS: *Picea sitchensis*, Sitka spruce, genetics, tree improvement, adaptation